SHORT COMMUNICATION

Substrate selection for web-building in *Cyrtophora citricola* (Araneae: Araneidae)

Ruth Madrigal Brenes: Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria Rodrigo Facio, San José, Costa Rica. E-mail: ruthymad@gmail.com

Abstract. In general, spiders that build long-lasting webs invest a larger amount of silk and consequently a larger amount of energy in their construction than those species that build ephemeral webs. It is expected that spiders that build long-lasting webs choose rigid substrates for web construction to help preserve their investment. I experimentally tested this prediction by confining *Cyrtophora citricola* (Forsskål 1775) (Coddington 1989) spiders (n = 32) in containers provided with firm and unstable substrates for the spiders to construct their webs. This experiment confirms that *C. citricola* strongly prefers firm substrates to which to attach its web when it must choose between a firm and an unstable substrate.

Keywords: Araneids, spiders, orb-web, web-substrate selection

The structure of the habitat can be important for spiders when they select sites to build their webs (Janetos 1986). The substrates selected by spiders for web construction vary across species, and this selection may be especially crucial for spiders that build long-lasting webs. Within araneids, those species with long-lasting webs in general use more silk and invest more time to construct denser webs and are not capable of ingesting and recycling a high percentage of the silk of old webs (Lubin 1986; Townley & Tillinghast 1988; Kawamoto & Japyassú 2008), in contrast to those araneid species that make typical, shorter lasting orbs and are capable of ingesting the silk of their webs. The higher investments of silk, time, and energy by spiders constructing long-lasting webs increase the cost of web relocation (Tanaka 1989), likely imposing strong selection on the behaviors associated with web site choice.

Orb-weaving spiders in the genus *Cyrtophora* construct webs that consist of dense, horizontal orbicular sheets of dry silk with an irregular tangle of dry threads above and below (Wheeler 1926; Lubin 1973). The webs are strong, long lasting, and infrequently rebuilt, and are repaired when damage occurs (Lubin 1973, 1980). Thus the spider's choice of appropriate substrates to which to attach the web is important in order to decrease the probability of damage to the web. This paper experimentally examines the selection of firm vs. unstable substrate as support for the construction of the web by *Cyrtophora citricola* (Forsskål 1775) (Coddington 1989).

I collected 32 adult females of *C. citricola* between April and November of 2009 in the Valle Central of Costa Rica (09°56'N, $34^\circ15'W$). 1 placed each spider in a cardboard frame ($27 \times 22 \times 18$ cm: width \times height \times depth); if a spider did not build its web within four nights, it was released and replaced with another spider.

Spiders do not usually attach silk threads to tightly stretched plastic wrapping material, so I covered the open, broad faces of the frame with this material. 1 also lined one of the sides of the frame with a sheet of this material and then hung a sheet of paper cut into 12 strips (height 22 cm, width 1.5 cm) in front of this side (Fig. 1). The opposite side was not lined with plastic wrapping material, thus giving the spider sufficient support to construct its web. Six of the strips of each sheet were attached to both ends (giving a firm substrate), and six were attached only to the upper end (giving an unstable substrate), following an alternate order: one strip attached to both ends (odd numbers in Fig. 1) followed by another strip attached to one end (even numbers in Fig. 1). I drew horizontal lines 2 cm apart that divided each strip into 11 sections (A to K, from top to bottom), allowing me to record the heights at which spiders attached threads (Fig. 1).

I gave each spider four nights to build its web (20 of the 32 spiders built a complete web in two nights, 12 more in the next two nights). After a spider wove the spiral, the tendency for an addition of new silk threads decreased drastically unless the web was damaged (G. Barrantes unpubl. data). On the fifth day, 1 used the coordinates provided by the numbered and lettered strips to record the location of each thread attachment. The tensions on the threads generally pulled the unstable strips out of their vertical alignment, toward the spider's web. After counting the threads, I fed the spider a fly, then cut all threads that were attached to the paper strips. This made the spider rebuild the orb of the web, though part of the scaffolding above the

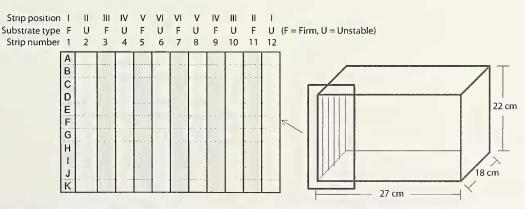


Figure 1.—Stylized drawing of the arrangement of the experimental strips to which spiders attached their threads. F = firm; U = unstable; positions of strips closest to the corners were I, and those nearest the center were VI.

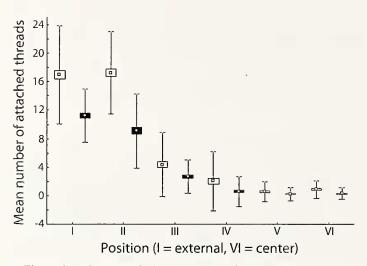


Figure 2.—Number of threads (mean, SE, and SD, n = 32) attached to firm strips (white boxes) and to unstable strips (black boxes), ordered from the external position (position I) to the center (position VI) (Firm substrate: B = -0.32, $R^2 = 0.82$, $F_{1,4} = 18.51$, P < 0.0001; Unstable substrate: B = -0.17, $R^2 = 0.70$, $F_{1,4} = 9.19$, P < 0.0001; comparing slopes, t = -7.36 P < 0.001). Spiders were more likely to attach threads to firm vertical surfaces. Furthermore, stable threads were more likely to be located in high and low positions, while unstable threads were more evenly distributed.

orb was not rebuilt (R. Madrigal Brenes pers. observ.). I repeated this procedure two more times and counted the threads of each of the three webs built by each spider. Webs were rebuilt within the next three nights in all cases.

To determine if spiders preferred to attach threads to the firm or the unstable strips, 1 first averaged for each spider the values corresponding to the three webs. I then compared the number of threads attached to pairs of strips at comparable positions in the cage (distances from the corners) using a paired *t*-test. I thus compared band 1 (firm) with band 12 (unstable); 2 (unstable) with band 11 (firm) (Fig. 1), and so on. To measure the distribution of threads relative to the position of the strips (horizontal axis, position 1 closest to the corner), I performed a regression for the firm strips and another one for the unstable strips and then eompared the slopes to determine if the number of threads changed relative to the position of the strips in firm vs. unstable strips.

Lastly, for both firm and unstable substrates, I determined if the spider attached different numbers of threads at different heights along the length of each strip, using a Kolmogorov-Smirnov test for each type of substrate. For this test, I averaged the number of threads attached to unstable and firm substrates at each height (sections from A to K) for each of the three webs of the spiders.

All spiders (n = 32) attached more threads to the firm strips than to the unstable strips (mean \pm SD: firm = 7.02 \pm 1.15, unstable = 4.04 \pm 0.85; paired $t_{31} =$ 18.96, P < 0.0001). However, spiders did not distribute their threads evenly along either the horizontal or vertical axes. Horizontally, all spiders attached more threads to the strips nearer the corners of the cage, regardless of whether the strip was firm or unstable (Fig. 2). Along the vertical axis, spiders attached higher numbers of threads to the upper portion of each strip, followed by intermediate numbers in the lowest portions, with the fewest threads attached to positions near the center of the strip (Kolmogorov-Smirnov test, D = 0.36, n = 11, P < 0.025; Fig. 3).

In this experiment *Cyrtophora citricola* showed a strong preference to attach silk threads to firm substrates. The ability to select firm substrates for web construction is probably important for this species, which builds long-lasting webs. The additional preference for attaching threads near the corners rather than to the central section

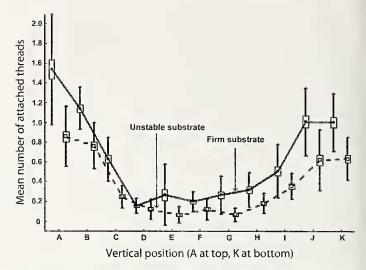


Figure 3.—Number of threads (mean, SE, SD) attached to the different vertical sections of the firm strips (solid line) and unstable strips (dotted line). Position A is at the top of the strip and position K at the bottom.

of the wall may be a consequence of the characteristics and shape of the orbs of this species. Orb-web building spiders tend to build long bridging lines that form part of the upper frame and support the rest of the orb web. In general, the attachment points of the anchor lines that support the frame are relatively few and tend to be well separated (Foelix 2011). Although construction behavior is yet unexplored in *C. citricola*, it is possible that this species follows a similar pattern of behavior: first build anchor and/or frame lines that are attached to extremes, and then use these lines as mechanical support to construct the rest of the web. This possibility remains to be demonstrated.

Based on an experimental approach, the results of this investigation demonstrated that *C. citricola* clearly selects firm over unstable substrates to construct its web. A similar approach may be used to test whether other spiders that construct durable webs such as species in the *Mecynogea* genus and Uloboridae family have a similar pattern of substrate selection, and to test whether spiders that construct less resistant and durable webs (e.g., *Leucauge* spp.) have a lower propensity to select firm substrates.

ACKNOWLEDGMENTS

I thank Gilbert Barrantes, William G. Eberhard, Linden Higgins and two anonymous reviewers for many helpful comments and statistical advice.

LITERATURE CITED

- Coddington, J.A. 1989. Spinneret silk spigot morphology: evidence for the monophyly of orbweaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. Journal of Arachnology 17:71–95.
- Foelix, R.F. 2011. Biology of spiders. Third edition. Oxford University Press, New York.
- Janetos, A.C. 1986. Web site selection: are we asking the right question? Pp. 9–22. In Spiders: Webs, Behavior, and Evolution. (W.A. Shear, ed.). Stanford University Press, Palo Alto, California.
- Kawamoto, T.H. & H.F. Japyassú. 2008. Tenacity and silk investment of two orb weavers: considerations about diversification of the Araneoidea. Journal of Arachnology 36:418–424.
- Lubin, Y.D. 1973. Web structure and function: the non-adhesive orbweb of *Cyrtophora moluccensis* (Doleschall) (Araneae: Araneidae). Forma et Functio 6:337–358.
- Lubin, Y.D. 1980. The predatory behavior of *Cyrtophora* (Araneae: Araneidae). Journal of Arachnology 8:159–185.

- Lubin, Y.D. 1986. Web building and prey capture in the Uloboridae. Pp. 132–171. *In* Spiders: Webs. Behavior, and Evolution. (W.A. Shear, ed.). Stanford University Press, Palo Alto, California.
- Tanaka, K. 1989. Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. Oecologia 81:459–464.
- Townley, M.A. & E.K. Tillinghast. 1988. Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the

addhesive spiral component, gabamide. Journal of Arachnology 16:303–319.

Wheeler, W. 1926. Social habits of some Canary Island spiders. Psyche 33:29–31.

Manuscript received 29 March 2011, revised 14 May 2012.